SHORTER ARTICLES AND CORRESPONDENCE

ON THE PROGRESSIVE INCREASE OF HOMOZYGOSIS IN BROTHER–SISTER MATINGS

IT has been brought to my attention that the note concerning inbreeding, written at the request of Mr. Phineas W. Whiting to add to his paper on "Heredity of Bristles in the Common Greenbottle Fly, *Lucilia Sericata* Meig.," which appeared in the AMERICAN NATURALIST for June, 1914, might be taken to mean that my data had been sent by Dr. E. M. East to Dr. Raymond Pearl by whom it had been published as his own. I wish to make it clear by a statement of the facts herewith that no such interpretation should be placed upon the note. I was seriously ill at the time and did not submit my manuscript to Dr. Castle or Dr. East for revision, as I should ordinarily have done. In that case no doubt, any ambiguity of statement would have been pointed out to me.

Mendel, in his original paper, showed that if equal fertility of all plants in all generations is assumed, and, furthermore, if every plant is always self-fertilized, then in the nth generation the ratio of any allelomorphic pair (A,a) would be $2^n - 1$ AA : 2 Aa : $2^n - 1$ aa. This statement was generalized in 1912 by East and Hayes[1] for any number of allelomorphic pairs. "The probable number of homozygotes and any particular class of heterozygotes in any generation r is found by expanding the binomial $[1 + (2^r - 1)]^n$ where n represents the number of character pairs involved. The exponent of the first term gives the number of heterozygous and the exponent of the second term the number of homozygous characters." A little later Jennings independently showed how homozygotes are produced from heterozygotes by self-fertilization.[2]

East and Hayes[3] published no generalized formula for calculating the reduction toward homozygosis through any other type of mating, but that this was thought to be a proper conclusion deducible from the above is shown by the following quotation (p. 21):

[1] U. S. Dept. Agr., Bur. Plant Ind., Bull. No. 243.
[2] AMER. NAT., August, 1912.
[3] *Loc. cit.*

Close selection, of course, tends toward the same end (homozygosis), but not with the rapidity or certainty of self-fertilization.

This idea is further shown by their statements under the heading "Extension of Conclusions to the Animal Kingdom" (pp. 39–43).

A little later Mr. Whiting had occasion to work out the results of random matings of brothers and sisters, in connection with his work at the Bussey Institution. He found that the amount of heterozygosis was reduced one eighth in matings of the F_2 generation and from this concluded that the remaining heterozygosis was reduced one eighth in each succeeding generation, so that in the nth generation the number of matings which would produce at least some heterozygous offspring would be $(7/8)^{n-1}$. He showed these figures to Dr. East, who agreed with the general conclusion (tendency toward homozygosis), but thought that the ratio would not hold for offspring after the F_3 generation. Dr. East, however, after a casual examination was not able to show Mr. Whiting the fallacy in his work and did not go into the matter further.

In the AMERICAN NATURALIST for October, 1913, Dr. Raymond Pearl criticized the extension of the conclusions for self-fertilized plants to the animal kingdom.[4] He applied the figures of Pearson, 1904,[5] for random matings, which show that the relative number of homozygotes and heterozygotes remains constant in a population where all factors of fertility, virility and environment have the same effect upon each individual in each generation. Dr. Pearl's error, as he has since recognized, lies in the fact that in the F_2 generation random mating involves only brothers and sisters, while in all subsequent generations it also involves other relationships.

When I read Dr. Pearl's article in October I naturally wondered why there was such a difference of opinion between Dr. East, Mr. Whiting and Dr. Pearl. Before finishing the article I computed the amount of homozygosis in the F_1 generation as 0 per cent.; in F_2, 50 per cent.; F_3, 50 per cent.; F_4, 62.5 per cent., and F_5, 68.25 per cent. As soon as possible after that I figured other generations until the heterozygosis would be reduced to one half of one per cent. of the maximum of heterozygosis in the

[4] East and Hayes, 1912, *loc. cit.*

[5] *Phil. Trans. Roy. Soc.* (A), Vol. 203, pp. 59 and 60.

F_1 generation and found that this was accomplished in the F_{25} generation, the amount of heterozygosis in each generation being:

F_6, 75.000 per cent.	F_{13}, 94.312 per cent.	F_{20}, 98.710 per cent.
F_7, 79.687 per cent.	F_{14}, 95.398 per cent.	F_{21}, 98.956 per cent.
F_8, 83.594 per cent.	F_{15}, 96.277 per cent.	F_{22}, 99.155 per cent.
F_9, 86.719 per cent.	F_{16}, 96.988 per cent.	F_{23}, 99.317 per cent.
F_{10}, 89.258 per cent.	F_{17}, 97.563 per cent.	F_{24}, 99.447 per cent.
F_{11}, 91.309 per cent.	F_{18}, 98.029 per cent.	F_{25}, 99.553 per cent.
F_{12}, 92.969 per cent.	F_{19}, 98.405 per cent.	F_{26}, 99.638 per cent.

With the approval of Dr. Castle and Dr. East I prepared to publish these figures.

Shortly after this Dr. Pearl wrote to Dr. East asking for an opinion upon his article. Dr. East, in the meantime, by a method differing from mine, had worked out the ratios independently. Before answering Dr. Pearl's letter, however, Dr. East compared his results with mine. They agreed. Dr. East then wrote to Dr. Pearl, giving a short rebuttal of Dr. Pearl's arguments, enclosing some of his own figures and adding that a student of Dr. Castle's (myself) was thinking of publishing the complete figures. Dr. Pearl immediately acknowledged his mistake and very generously asked if he should wait until I had published my article before he published a correction. Dr. East replied that he could see no reason for delaying the correction and advised me of this reply.

Since it seemed proper for Dr. Pearl to correct his previous article, I decided to withhold my own figures and incorporate them later in a paper bearing also upon other matters. Dr. Pearl's second article came out in the AMERICAN NATURALIST for January, 1914, and this paper together with the third article in the same journal for June, 1914, shows that his work was entirely independent of Dr. East's or my own.

When Mr. Whiting asked me for a note giving the figures showing what might be expected in the way of an automatic increase in homozygosity when brothers were mated with sisters in successive generations, as Mr. Whiting had done with his flies, I naturally was pleased to have him accept my figures as correcting his own, and at the same time give me an opportunity to acknowledge my indebtedness to those who furnished the idea upon which my figures were based.

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